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RESEARCH ARTICLE

Updating the distribution of *Vampyrum spectrum* (Chiroptera, Phyllostomidae) in Colombia: new localities, potential distribution and notes on its conservation

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Abstract

The Spectral Bat (*Vampyrum spectrum*) is classified as Near Threatened by the International Union for Conservation of Nature. In Colombia, it has not been included in any risk assessments, because

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it is a poorly documented species in the country. Using new occurrence data and ecological niche modelling we evaluate the distribution and analyze the species' ecological and conservation needs in Colombia. With the new records, *V. spectrum* shows a distribution over six biogeographic provinces in the country, along an elevational range between 96 and 1750 m. The Spectral Bat has been reported in a wide variety of ecosystems from dry forest and fragmented landscapes, to forested areas. Predictive models suggest a wider presence of this species in the west of the country, center, and southern Andes. The limited number of specimens limits our attempt to evaluate morphometric variation among Colombian populations; however, we detect a variation in the mean value of the forearm and ear length regarding northeast South American populations. Areas with the greatest potential distribution detected in this study could be prioritized in conservation strategies, and make plans accordingly for this and other species that coexist in its range. Finally, we highlight the low representativeness of Protected Areas for the Spectral Bat and add some ecological notes about this rare species.

Keywords

Carnivorous bat, ecological niche modelling, Phyllostominae, Protected Areas, rare species, Spectral Bat

Introduction

The Spectral Bat *Vampyrum spectrum* (Linnaeus, 1758) is the largest bat species in the Neotropical region. It has a wide distribution ranging from southern Mexico to northern and central Bolivia (Da Silva and Rossi 2011; Acosta et al. 2019), east to the Amazon and central and northern Brazil (Nunes et al. 2005; Nogueira et al. 2007; Sousa et al. 2016). Despite its wide distribution, it is considered a rare species due to its low abundance and scarce representation in biological collections (Greenhall 1968; Solari 2018). Little is known about its natural history, ecology, and population dynamics (Acosta and Azurduy 2006; Acosta et al. 2019). It inhabits well-preserved environments (Solari 2018), where it acts as a top predator of small birds and mammals (rodents and bats), and possibly its diet includes some insects and fruits too (Peterson and Kirmse 1969; Navarro and Wilson 1982; Bonato et al. 2004; Gardner 2008). In addition, some studies have provided information on its echolocation, home range (Vehrencamp et al. 1977), and local distribution (Sousa et al. 2016; Esquivel and Rodríguez-Bolaños 2018).

Globally, the Spectral Bat is listed as Near Threatened (NT) according to the IUCN Red List (Solari 2018) due to population decline associated with loss and fragmentation of natural habitats (Aguirre et al. 2008). In Colombia, as in other countries, there are relatively few records, limiting our knowledge about its actual distribution and conservation status. The first record for Colombia was made by Hall and Kelson (1959) based on one specimen collected at "El Boquerón (de Napipi), Chocó (6°43'N, 77°30'W)", however, this locality is actually located in Panama, causing confusion about the species presence in Colombia (Aellen 1970; Gardner 2008). Later, Cuervo et al. (1986) included *V. spectrum* as present in humid forest up to 2800 m a. s. l. in Colombia, but they provided no additional information. Alberico et al. (2000) followed Cuervo et al. (1986) by including the species in an elevational range between 0 to 2800 m, and mentioned voucher specimens in the collections of the Instituto de Investigaciones Biológicas Alexander von Humboldt (IAvH), Villa de Leyva and the Instituto de Ciencias Naturales (ICN), Bogotá.

Since then, the presence of the species has been confirmed in different geographic regions of Colombia including: i) The Andean Region: departments of Antioquia (Cuartas-Calle and Muñoz-Arango 2003), Caldas (Castaño et al. 2003; Escobar-Lasso et al. 2013), Cauca (Ramírez-Chaves and Pérez 2010), Huila (Rivas-Pava et al. 2007), Tolima (Maria 2004; Gutiérrez-Díaz et al. 2010; García-Herrera et al. 2019; Esquivel et al. 2020), Nariño (Ramírez-Chaves and Noguera-Urbano 2010), Cundinamarca, and Valle del Cauca (Mantilla-Meluk et al. 2009). ii) The Amazon Region: departments of Amazonas (Montenegro and Romero-Ruiz 1999; Rojas et al. 2004; Mantilla-Meluk et al. 2009), and Caquetá (Montenegro and Romero-Ruiz 1999; Marín-Vásquez and Aguilar-González 2005). iii) The Pacific Region: Department of Chocó (Asprilla et al. 2016). iv) The Caribbean Region: departments of Sucre (Cabrera 2011) and La Guajira (Esquivel and Rodríguez-Bolaños 2018), and v) the Orinoquian Region: departments of Meta and Vichada (Mantilla-Meluk et al. 2009; Esquivel and Rodríguez-Bolaños 2018). However, the elevational range distribution is not clearly defined, and has been mentioned as occurring from 0 to 2800 m (Cuervo et al. 1986; Alberico et al. 2000), from 10 to 1065 m (Mantilla-Meluk et al. 2009), and from 10 a 2150 m (Solari et al. 2013).

Correlative environmental niche modelling (ENM) attempts to model a species' relationship with environmental variables and predict habitat suitability for that species based on known observations of its presence. Although ENM techniques are inherently limited by imperfect knowledge, they have nonetheless proven extremely useful in assessing the effectiveness of Protected Areas distribution (Catullo et al. 2008), assessing species' vulnerability to proposed local land use change (Santos et al. 2013), predicting distributions of rare species (Marino et al. 2011; Rheingantz et al. 2014) and possible responses to climate change by species and ecosystems (Moor et al. 2015; Sobral-Souza et al. 2018). Due to the limited information on the distribution of *V. spectrum* in Colombia, environmental niche models could be extremely useful for predicting the distribution of this species in several areas of the country. In addition, a predictive model of its distribution could be calculated based not only on records gathered from this country, but also from other nations in its range.

In this study we (1) report new localities of *V. spectrum* from the Andean, Caribbean and Orinoquian regions, (2) update the distribution of the species in Colombia, (3) use the distribution data together with Ecological Niche Modelling (ENM) to generate a map of the potential distribution of the species, and (4) include information on its morphometric variation, conservation status and some ecological notes that contribute to the knowledge of this rare species.

Material and methods

Occurrence data

We compiled a dataset of occurrence records of the Spectral Bat *V. spectrum* throughout its entire distribution in the Neotropics by searching in on-line databases including the Arctos database (Conroy 2020), Global Biodiversity Information Facil-

ity (https://www.gbif.org/), Instituto Chico Mendes database (https://www.icmbio.gov.br/portal/), Mammal Networked Information System (http://manisnet.org/), Sistema de Información sobre Biodiversidad de Colombia (https://sibcolombia.net/), and SpeciesLink (http://www.splink.org.br/). Also, we search records from literature as articles and notes from Scopus (https://www.scopus.com/home.uri), ISI Web of Knowledge (https://www.webofknowledge.com/) and Google Scholar (https://scholar.google.com/) using the following keywords in Spanish, English and Portuguese: "Vampyrum spectrum", "Spectral Bat", "Linnaeus false vampire bat", "false vampire" and "Phyllostominae". We assigned latitude/longitude to the localities without coordinates based on site descriptions by collectors, and plotted the locations with Global Gazetteer Version 2.3 (http://www.fallingrain.com [Accessed August 2020]) and Google Earth (https://earth.google.com/web/ [Accessed August 2020]). We standardized the geographical coordinates with ArcGis 10.3 and converted to decimal degrees using the WGS84 global reference system. Quality control filters were applied to this dataset to reduce the effect of spatial, temporal and taxonomic errors using CoordinateCleaner, a package for the automated cleaning of occurrence records from biological collections (Zizka et al. 2019) with R program, version 4.0.2 (R Development Core Team 2020).

To update the distribution of *V. spectrum* in Colombia, we also reviewed specimens from biological collections (Appendix 1), and unpublished photographs in which the picture unambiguously allowed its identification. We associated the records with the eco-regions and biogeographic provinces of Colombia (Hernández-Camacho et al. 1992; Dinerstein et al. 2017).

Ecological niche modelling (ENM)

To adequately characterize the *V. spectrum*'s environmental niche, we took 183 occurrence points from its entire neotropical distribution and thinned them by 5 km to reduce spatial autocorrelation – distance based on home range (Vehrencamp et al. 1977) – using SDMToolbox in ArcGIS (Brown 2014). We selected environmental variables a priori based on ecological relevance to the species. Maximum temperature of the warmest month (Bio05) and precipitation of the driest month (Bio14) were taken from the bioclimatic variables at WorldClim (Fick and Hijmans 2017), while the percentage of evergreen broadleaf forest cover (hereafter Forest Cover) (Tuanmu and Jetz 2014) and the Global Multi-resolution Terrain Elevation Data – slope (GMTED) (Amatulli et al. 2018) were sourced from the EarthEnv system. We chose these four variables due to their relevance to bat species – for example, high maximum temperatures could induce thermal stress in *V. spectrum*, whilst slope and evergreen broadleaf forest cover could affect habitat provision and hunting success. We imported all masked variables to R version 4.0.2 (R Development Core Team 2020), and tested for multicollinearity using VIF tests and pairwise plots. Highly correlated variables (VIF score > 10 or Pearson correlation > 0.7) were elim-

inated one at a time, starting with the variable(s) deemed to possess the least ecological relevance to *V. spectrum*. To help create more reliable predictions, we used multiple modelling algorithms together in an ensemble modelling approach using the sdm package (Naimi and Araujo 2016). The model combination included Maxent, Boosted Regression Tree (BRT), Support Vector Machine (SVM) and Random Forest (RF). Ten cross-validation replications were performed (where the replicate points were divided into equal folds of test and training points). Threshold values to assign binary presence/absence were calculated based on the suitability that would maximize the sum of sensitivity and specificity. We assessed the models using true skill statistic (TSS score > 0.4) and area under the receiver-operating curve (AUC score > 0.7). Model predictions were weighted by TSS in the creation of the final ensemble maps to ensure reliability of the final map, thus the models with the highest TSS score have the strongest influence on the final map output. Although the model was trained using *V. spectrum*'s entire present distribution (we used a training extent equal to the IUCN distribution map for the species buffered by 250 km to include new known presence points), the map only provided predictions for Colombia. In addition to map creation, variable importance was also calculated using both Pearson correlation and AUC metrics (in both cases, results were obtained using the permutation method, where the model assesses the effect of removing one variable at a time).

The final ensemble map was reclassified using the binary threshold. This binary map was then further filtered in ArcMap v10.6 to exclude "above threshold" pixels in areas above 2000 m a. s. l (taking into account that 1750 m is the maximum elevation for *V. spectrum* in Colombia), using the GMTED elevation dataset (Amatulli et al. 2018). This was done to provide an estimate of *V. spectrum*'s distribution in Colombia and potentially assist future research or conservation action planning. To calculate the suitable habitat area in Colombia, we converted the elevation filtered binary thresholded map to an equal area projection, using the South America Albers Equal Area Projection. Finally, in order to calculate the suitable habitat area of *V. spectrum* within Colombian Protected Areas (PAs) we overlapped our output map with PAs shapefiles. Distribution of Colombia's Protected Areas was based on the World Database on Protected Areas (WDPA; http://www.protectedplanet.net), which contained six classes (I–VI) of Protected Areas categorized by the World Conservation Union (Dudley et al. 2013).

Morphometric data

We took external (N = 3) and craniodental (N = 13) measurements using digital calipers of 0.01 mm accuracy, following Simmons and Voss (1998). Standard external measurements (HF, hind foot length and E, ear length) were taken from skin labels or database records. Other measurements are as follows: Forearm length (FA), Greatest length of the skull (GLS), Condyloincisive length (CIL), Condylocanine

length (CCL), Zygomatic breadth (ZB), Maxillary toothrow length (MTRL), Mandibular toothrow length (MANDL), Postorbital breadth (PB), Braincase breadth (BB), Braincase height (BH) without the sagittal crest, Palatal length (PL), Canine-Canine breadth (C-C), Superior Canine length (SCL) and Inferior Canine length (ICL) both considered in teeth without wear. We calculated descriptive statistics (mean and range) for all Colombian specimens.

Results

In Colombia, *Vampyrum spectrum* is known from 37 records in 15 departments along six biogeographic provinces: a) Peri-Caribbean Arid Belt, b) Orinoco, c) Guyana, d) Amazonia e) Chocó-Magdalena and f) Nor-Andean. Likewise, the species has been recorded in different ecoregions as Montane forests (19 records), Moist forests (8), Dry forests (4), Llanos (4) and Xeric scrub (2). Based on vouchers, the Spectral Bat is distributed in an elevational range between 96 and 1750 m, with most records (67.5%; N = 25) below 600 m. Of the total, four are new localities, recently obtained in fieldwork activities (Fig. 1; Table 1) and presented below.

The first record from Mutatá, Department of Antioquia – north Urabá subregion, "Vereda" Chontadural (7°13'50.4"N, 76°26'58.8"W; 163 m a. s. l) – is a specimen found as a result of a biological characterization in a requirement for obtaining environmental permits for the development of a mining project (stone), in June 2019. The specimen is an adult male (CZUC-M 0409), found entangled in a wire fencing at ground level on a gutter created for runoff. Because the skin was already totally destroyed, with only the skull preserved, a fracture in the braincase was presumed to be the cause of death. The area containing this specimen was a wooded cover of tropical humid forest (bh-T) crossed by the Caño Bijará, where secondary vegetation prevails with a wide canopy providing spaces for the species' flight capacity. The second record comes from Paz de Ariporo, Department of Casanare (5°29'24.36"N, 71°7'4.79"W; 330 m a. s. l), and corresponds to an adult male captured as result of a biological characterization during 2017. The specimen was photographed and then released in the same area, which has gallery forests and extensive plains. The third record comes from San Alberto, Department of Cesar (7°45'0"N, 73°22'58.7"W; 125 m a. s. l); it is an individual found in the development of a biological characterization during 2015. The individual corresponds to an adult female recorded in a gallery forest fragment, in a very narrow strip of secondary vegetation on the banks of a stream, near to oil palm crop. The area where this specimen was found is strongly pressured by the oil crop, but there are still some remnants of gallery forest that allow the survival of the species. The fourth record comes from the municipality of Gualanday, Department of Tolima (4°17'24"N, 75°2'9.6"W; 541 m a. s. l), and represents an adult female found as a result of the development of an environmental impact study during 2015. The individual was recorded by Tatiana Toro-Sánchez in a dry tropical forest remnant near water bodies and agricultural crops (Fig. 2).

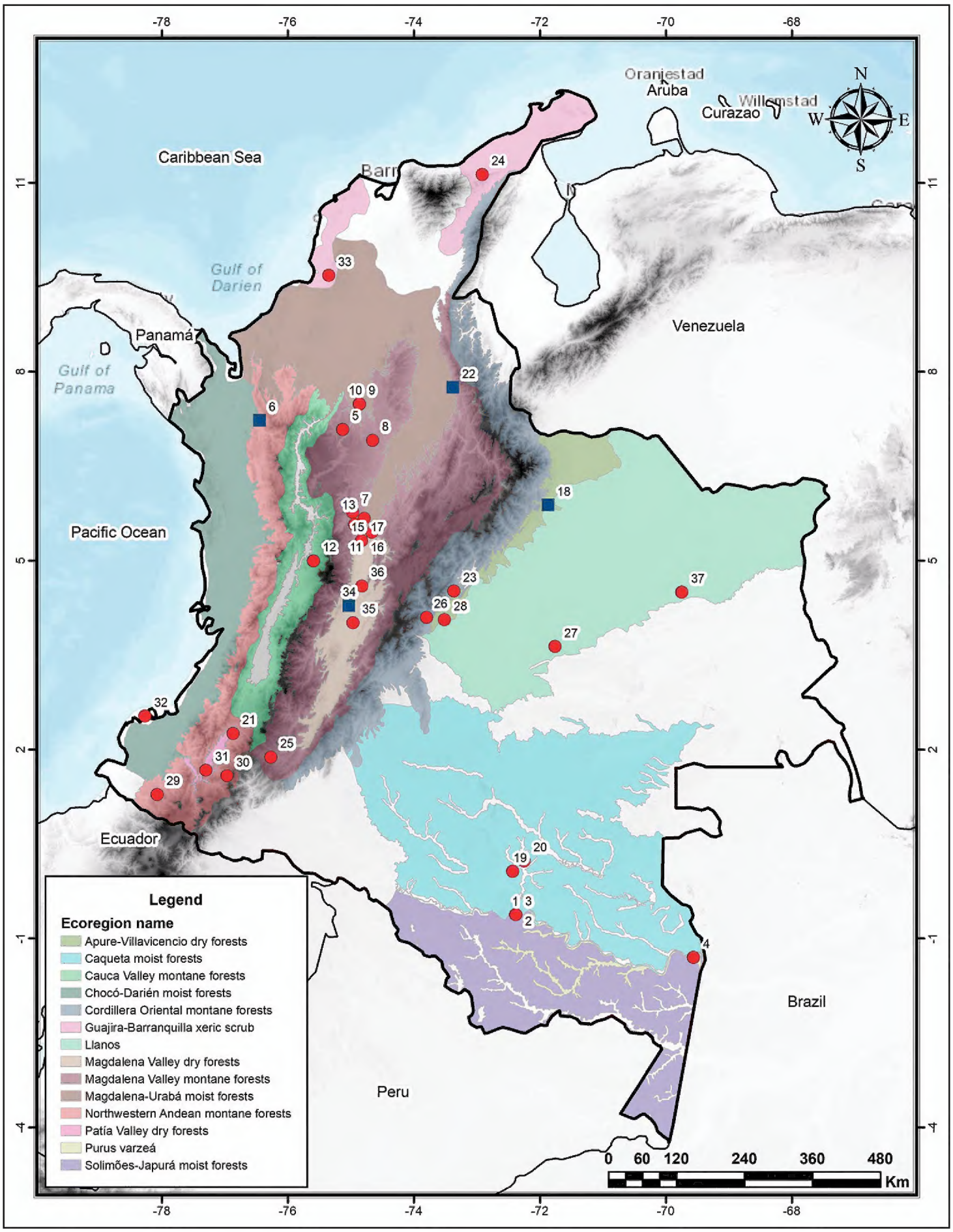

Figure 1. Localities of records of *Vampyrum spectrum* in Colombia. Red circles show previous records and blue squares show the new records. The numbers correspond to those described in Table 1.

Ecological niche modelling

Our models had a mean TSS (0.49 for BRT, 0.48 for Maxent, 0.47 for RF and 0.46 for SVM) and mean AUC (0.78 for BRT, 0.76 for Maxent, Random Forest and

Table 1. Records of *Vampyrum spectrum* in Colombia. * indicates new records and *** indicate the highest record in the country. Acronyms: Colección Teriológica Universidad de Antioquia (CTUA), Colección Zoológica Universidad de Córdoba (CZUC), Colección Zoológica Universidad del Tolima (CZUT-M), Colección de Mamíferos Instituto Alexander von Humboldt (IAvH), Colección de Mamíferos del Instituto de Ciencias Naturales (ICN), Muséum d'histoire naturelle de la Ville de Genève (MHNG), Colección Mastozoológica del Museo de Historia Natural de la Universidad del Cauca (MHNUC), Museo de Historia Natural Universidad de Caldas (MHN-UCa), Museo de La Salle-BOG (MLS), National Museum of Natural History (NMNH), Colección Zoológica Universidad de Nariño (PSO-CZ), and Colección de Mamíferos Universidad del Valle (UV).

	Coordinates (Latitude, Longitude)	Department	Locality	Record Year	Elevation (m.a.s.l)	Reference	Records from museums
1	-0.6217, -72.384	Amazonas	Araracuara: Hospital	1977	192		ICN 6407
2	-0.6217, -72.384	Amazonas	Araracuara: Hospital	1977	192		ICN 6408
3	-0.6217, -72.384	Amazonas	Colonia de Araracuara	1961	200	Esquivel and Rodríguez-Bolaños (2018)	ICN 176, MHNG 1930.069
4	-1.3003, -69.564	Amazonas	Corregimiento La Pedrera; Rio Caquetá, Quebrada El Ayo	2001	96		ICN 21168
5	7.0833, -75.133	Antioquia	Anori			Muñoz (2001)	
6*	7.2307, -76.450	Antioquia	Corregimiento Pavarando Grande; Vereda Chontadural	2019	163	This study	CZUC-M 0409
7	5.7668, -74.974	Antioquia	Vereda Campo Alegre; Predios de Don Guillermo Garcés	2016	646		CTUA 3404
8	6.9114, -74.657	Antioquia	Vereda La Cruz; Finca La Brillantina	2009	550		CTUA 4652
9	7.4833, -74.867	Antioquia	Zaragoza; 25 Km S La Tirana	1972	520		IAvH-M 3330
10	7.4870, -74.868	Antioquia	Zaragoza; Providencia	1972	410		IAvH-M 3331
11	5.4500, -74.667	Caldas	La Dorada			Muñoz (2001)	
12	4.9969, -75.594	Caldas	Manizales; Reserva Planalto	2007	1350	Escobar-Lasso et al. (2013)	MHN-UCa 959
13	5.6689, -74.788	Caldas	Norcasia; Vereda Quiebra de Roque	2010	250		MHN-UCa 989
14	5.5729, -74.940	Caldas	Norcasia; Vereda Monte Bello	2015	505		MHN-UCa 1478
15	5.3161, -74.833	Caldas	Victoria; Carretera Victoria-Mariquita; Vereda El Llano	1967	285	Castaño et al. (2003)	ICN 1680
16	5.3161, -74.833	Caldas	Victoria; Carretera Victoria-Mariquita; Vereda El Llano	1967	285	Castaño et al. (2003)	ICN 1681
17	5.3161, -74.833	Caldas	Victoria; Carretera Victoria-Mariquita; Vereda El Llano	1967	285	Castaño et al. (2003)	ICN 1682
18*	5.4901, -71.118	Casanare	Paz de Ariporo; El Desengaño	2017	330	This study	Photograph by Jhon Amaya
19	0.0667, -72.433	Caquetá	PNN Serranía del Chiribiquete; Rio Mesay, Puerto Abeja	2001	240		IAvH-M 7211
20	0.2322, -72.250	Caquetá	Rio Mesay; Chorro Mazaca	1995	240	Montenegro and Romero-Ruiz (1999); Marín-Vásquez and Aguilar-González (2005)	ICN 14702
21	2.2564, -76.869	Cauca	Coconuco			Ramírez-Chaves and Pérez (2010)	ICN 177

	Coordinates (Latitude, Longitude)	Department	Locality	Record Year	Elevation (m.a.s.l)	Reference	Records from museums
22*	7.7500, -73.383	Cesar	San Alberto	2015	125	This study	Photograph by Luz Myriam Moreno Bejarano
23	4.5167, -73.367	Cundinamarca	Medina; Granja Experimental Agropecuaria	1986	520		ICN 9527
24	11.1333, -72.917	Guajira	Riohacha; Corregimiento Tomarrazon Vereda Colon, Arroyo Los Coquitos	2011	170	Esquivel and Rodríguez-Bolaños (2018)	ICN 21382
25	1.8808, -76.270	Huila	San Agustín	1952	1700	Rivas-Pava et al. (2007)	MHNUC M042E
26	4.1000, -73.800	Meta	Acacías; Manzanares 20 Km suroccidente Villavicencio	< 1990		Eisenberg et al. (1989)	
27	3.6350, -71.761	Meta	Puerto Gaitán; vereda Alto de Tillavá, finca Los Cayenos	2015	174	Esquivel and Rodríguez-Bolaños (2018)	Photography
28	4.0626, -73.515	Meta	Villavicencio; Hacienda El Hachón Km. 16 carretera Puerto López	1982			ICN 8389
29	1.2866, -78.074	Nariño	Barbacoas; Reserva Natural Rio Ñambi	2004	1450	Ramírez-Chaves and Noguera-Urbano (2010)	UV 13281
30* **	1.5833, -76.967	Nariño	Ricaurte; Reserva Natural La Planada	1984	1750	Ramírez-Chaves and Noguera-Urbano (2010)	PSO-CZ 477
31	1.6741, -77.302	Nariño	Taminango; Remolino, El Algodonal	2013	570	Cabrera-Ojeda et al. (2016)	PSO-CZ 663
32	2.5333, -78.267	Nariño	Tola; Parque Nacional Natural Sanquianga	2000			UV 13282
33	9.5298, -75.352	Sucre	Coloso; Estación meteorológica primates	2012	300	Cabrera (2011)	No voucher
34*	4.2900, -75.036	Tolima	Gualanday	2015	541	This study	Photograph by Tatiana Toro-Sánchez.
35	4.0167, -74.967	Tolima	Guamo; Monte Cañada	1968	320	Maria (2004)	MLS 1540
36	4.5996, -74.829	Tolima	Piedras; cuenca Rio Totaré Vereda La Manga de los Rodríguez	2007	270	Gutiérrez-Díaz et al. (2010); Esquivel et al. (2020)	CZUT-M 0771
37	4.5000, -69.750	Vichada	Santa Teresita	1967	162		NMNH 431786

SVM) indicating the models fit well to the data. All individual model runs had values above our minimum accuracy values also. The relative habitat suitability for *V. spectrum* in Colombia based on our models, and the areas converted into a binary threshold and subsequently filtered to remove areas above 2000 m in elevation, are shown in Fig. 3A, B, respectively. The outputs indicate that habitat suitability across Colombia based on ENM ensemble was generally predicted to be much higher in the west of the country, in the Central Andes and the departments of the southern Andes.

Figure 2. Individual of *Vampyrum spectrum* captured in Gualanday, Department of Tolima, Colombian Central Andes. Photo by Tatiana Toro-Sánchez.

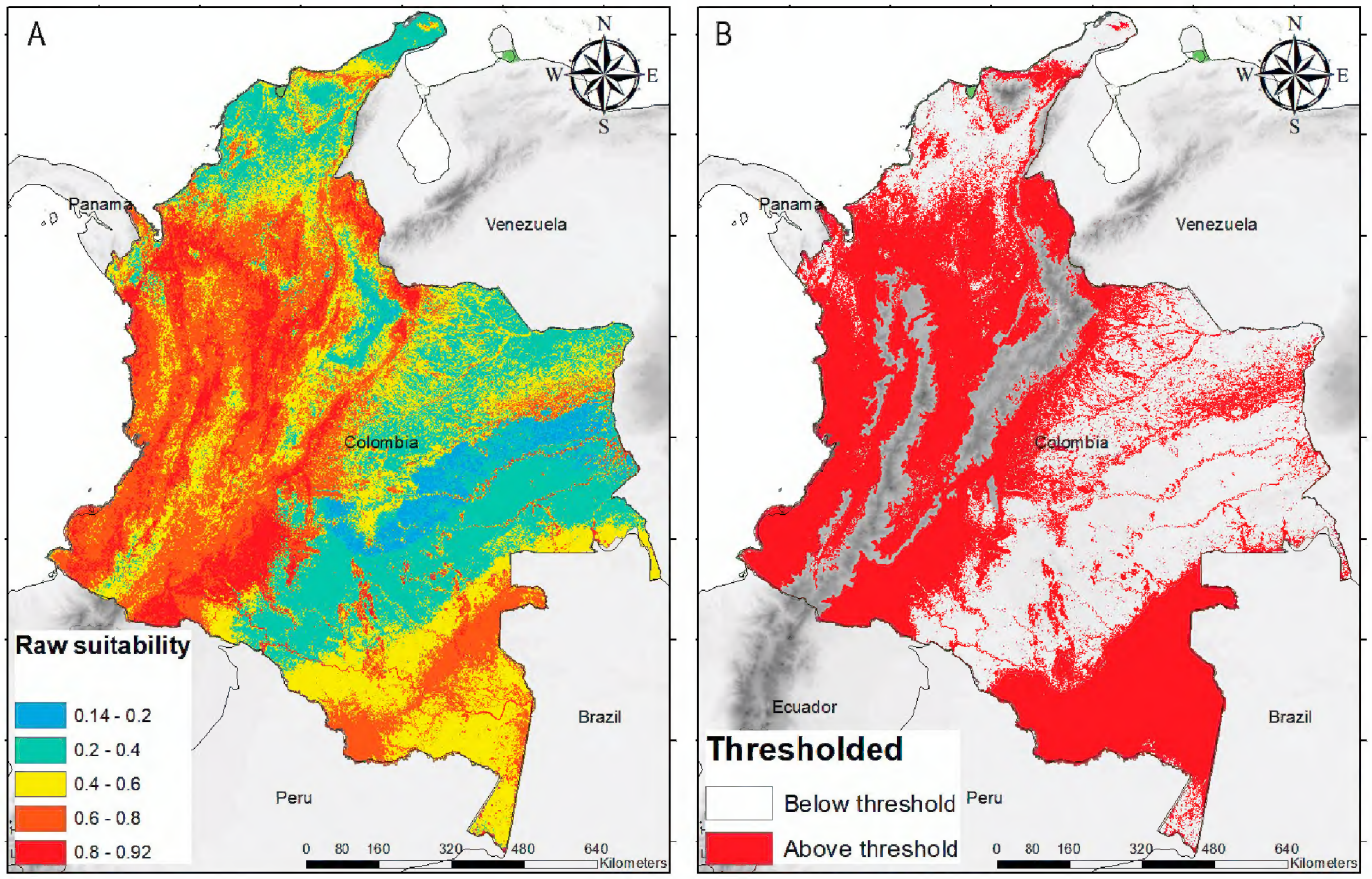

Figure 3. **A** Potential distribution of Spectral Bat *Vampyrum spectrum* in Colombia using an ensemble modelling approach with five different algorithms. Blue to red color scales indicate less to greater suitability area for the species. **B** Ensemble suitability map converted to a binary of above (suitable) and below (not suitable) threshold, manually reclassified to exclude high elevation areas (>2000 m a. s. l). Areas considered suitable were focused in the west and south of the country, although eastern Colombia also had significant areas above the threshold.

Table 2. Mean variable importance scores across all models and replicates.

Variable	AUC metric	Pearson correlation
Bio05	12.8	7.1
Bio14	40.4	19.7
EDForest	53.7	29
Slope	17.6	7.5

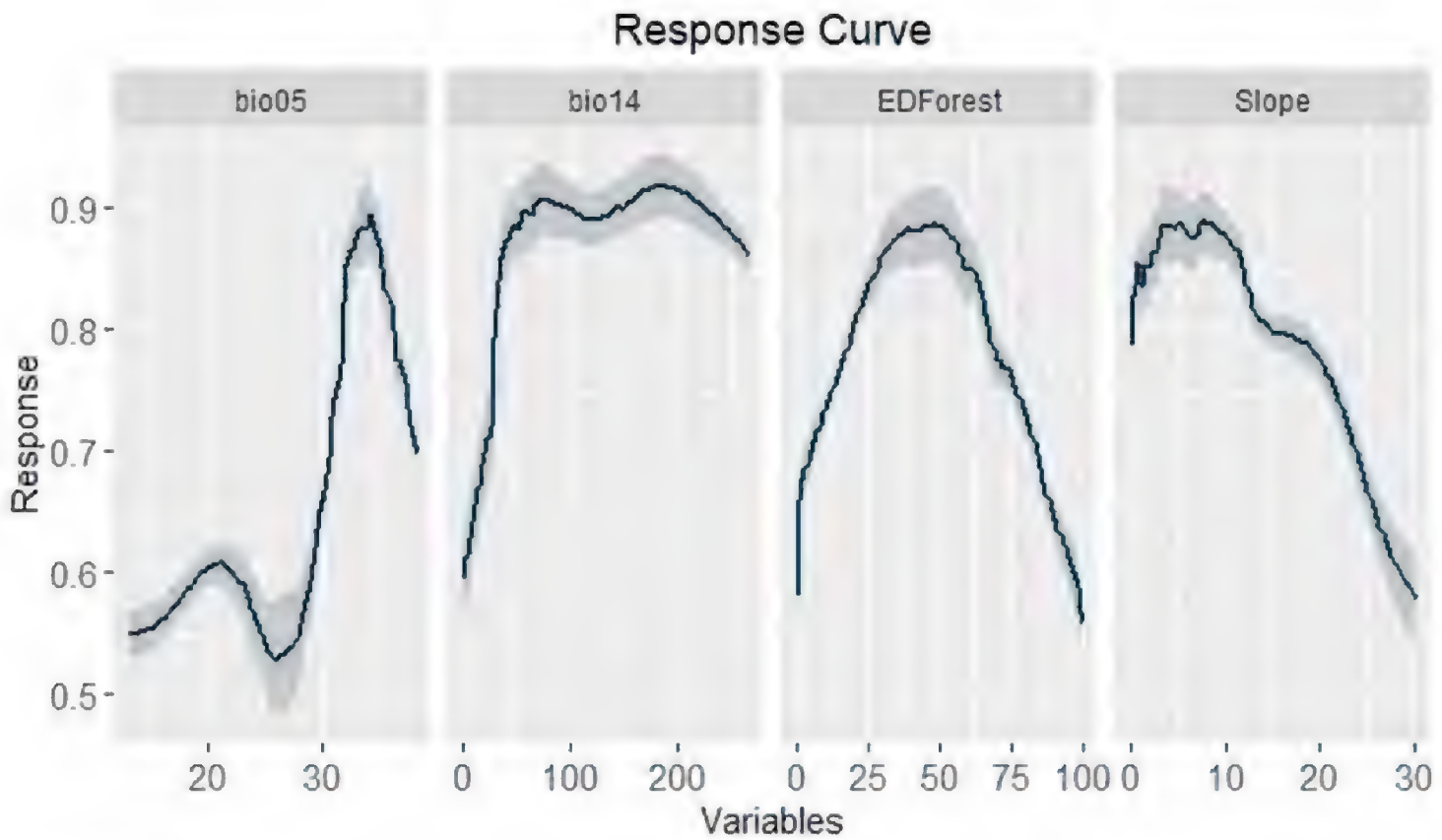

Figure 4. Variable response curves for *Vampyrum spectrum*. High values for temperature (bio05) and slope are related to less available habitats for the species.

Regarding variable importance, although the degree of importance differed between the two importance assessment metrics (TSS/AUC), the order was constant in both. Under both importance assessment methods, forest cover was by far the most important variable, followed by Bio14 (precipitation in the driest month), then slope, and finally Bio05 (maximum temperature of the warmest month) (Table 2). Suitability for *V. spectrum* declined sharply in very high temperatures (> 35 °C approximately), whilst higher precipitation increased suitability. Areas with high slope were less suitable for the species and the forest cover generally had a positive relationship with suitability, although this one decreased after 65% approximate forest cover (Fig. 4).

Morphometric data

The limited number of specimens limits our attempt to evaluate morphometric variation among Colombian populations. In general, the external and craniodental values were similar between specimens from Colombia, Central America and northeast South America (Guyana, French Guyana, Suriname and Trinidad). Despite that, we observed subtle differences in the length of the forearm mean value, and

– notably – the ear length that were larger in Colombian populations (Table 3). Among the 25 skulls reviewed, we found one specimen with polyodontia, showing an additional premolar in the right maxilla. This type of anomaly has been recorded in other Phyllostomid bat species (Esquivel et al. 2017).

Ecological and conservation notes

V. spectrum has been reported in a wide variety of ecosystems in the country. In the Andean region, most of the reviewed specimens were captured in areas with secondary vegetation and with strong human intervention. Some specimens were found in fragmented forest with the presence of cattle, selective felling and crops, and others have even been found dead resulting from their impact with High Voltage Transmission Lines in Antioquia (Instituto Alexander von Humboldt – IAvH 3330) and Caldas (Museo de Historia Natural de la Universidad de Caldas – MHN-UCa 959). Other records in the Andes show the presence of the species in ecosystems as tropical dry forest (Tolima), secondary forest, sub-Andean forest and premontane wet forest. In the Caribbean region, this species has been reported in secondary vegetation, gallery remnants and well-preserved areas in the foothills of the Sierra Nevada de Santa Marta (Instituto de Ciencias Naturales – ICN 21382), and in humid tropical remnants with well-preserved areas in Sucre. In the Orinoquia region, it occupies areas of primary forest, and finally, in the Amazonian region, it has been reported in Tepuyes forest (IAvH 7211), and primary forest (National Museum of Natural History – NMNH 431786).

Table 3. External and cranial measurements (in millimeters) of *Vampyrum spectrum* in Colombia. Mean, range and number individuals are shown. * Data from specimens in museums and literature: Goodwin and Greenhall (1961), Husson (1962), Gardner et al. (1970), Swanepoel and Genoways (1979), Simmons and Voss (1998). ** Subtle differences observed. Here, northeast South America includes specimens from Guyana, French Guyana, Trinidad and Suriname.

Measurements	Specimens from		
	Colombia	Central America*	Northeast South America*
FA**	108.7 (104–115) 16	104.8 (95.1–110.4) 9	103.9 (100–107.1) 12
E**	41.6 (39–45.7) 18		36.0 (30–40) 6
HF	30.9 (27.6–34.4) 17	32.8 (31–35) 7	30.0 (29–31) 6
GLS	51.4 (49.29–53.4) 16	51.4 (48.1–53.6) 10	51.4 (49.2–53.3) 13
CIL	43.1 (41.05–44.51) 14		43.2 (41.6–44) 7
CCL	42.4 (40.49–45.04) 12		43.1 (41.8–43.7) 7
ZB	24.1 (23.43–24.47) 15	24.2 (23.1–25.4) 9	24.0 (23.2–25.2) 12
MTRL	19.3 (17.11–21.23) 16	20.6 (19.7–21.7) 11	21.0 (20.6–21.5) 5
MANDL	21.5 (18.59–23.75) 15		
PB	8.1 (7.65–8.06) 17	8.1 (7.8–8.6) 9	7.9 (7.3–8.6) 13
BB	16.7 (14.02–19.15) 14	16.2 (15.6–18.2) 5	15.9 (15.7–16.5) 8
BH	17.7 (15.5–18.37) 13		
PL	24.6 (23.15–26.8) 15		24.8 (23.7–26.1) 7
C-C	8.7 (7.46–9.25) 14		
SCL	8.0 (7.43–8.76) 13		
ICL	8.4 (7.92–9.15) 13		

Our model predicted that currently around 13% of total habitat suitability area of *Vampyrum spectrum* are included within Protected Areas in Colombia. These Protected Areas are mainly concentrated in the Andean, Orinoquia and Amazonia regions. However, at a regional scale, the representativeness of these areas remains very low. PAs barely cover 12.8 and 8.4% of the suitable area in Andean and Orinoquia regions respectively while in the Caribbean region this value is even lower and only reaches 7.6%.

Discussion

Vampyrum spectrum presents a wide but discontinuous distribution in Colombia, probably related to its low detection. Information about this species is limited and mainly restricted to vouchers' records in natural history collections. From the first record in 1952 (Museo de Historia Natural de la Universidad del Cauca – MHNUC M042E) until 2020 only 37 records have been obtained. Although this number is low, when we analyze their temporality, we find that 70.2% were made before the year 2010, and in areas that are currently deforested, as in Tolima [reported in Guamo by Niceforo Maria in 1968, (Maria 2004)], Antioquia (in Zaragosa by N. Peterson in 1972), Caldas [via La Victoria-Mariquita by E. Osorno and A. Morales in 1967, (Castaño et al. 2003)], among others.

The number of records occurring after 2010 (N = 11), indicate the presence of the species in well-preserved areas in Amazonas, Caquetá, Meta, and Nariño, and its subsistence in patches of forest with strong anthropogenic pressure in the Central Andes. Although efforts are required to determine the state of the populations and confirm their presence in other areas, it is possible that the populations of the Andes and, in particular, northern Colombia, are most threatened given the high rates of deforestation that affect these regions (Etter et al. 2006). The habitat loss and fragmentation, and transformation of natural environments may disconnect populations, favoring possible local extinction events (Lino et al. 2019). Furthermore, intentional killings at the hands of local people who perceive bats as a threat, as occurs for other species of bats, could be causing the loss of a considerable number of individuals, mainly associated with the lack of knowledge and disinformation of the ecosystem services they provide (O'Shea et al. 2016; Bhattacharjee et al. 2018).

In Colombia, there is little information about the ecosystems occupied by *V. spectrum*. Herein, we recognize it in diverse ecosystems, but mainly associated with primary and secondary forests (Cabrera 2011; Esquivel and Rodríguez-Bolaños 2018), tropical dry forests (Maria 2004), and sub-Andean forests. Information about habitat preferences in the western region of the country is scarce, but, curiously, this area is predicted to have the most habitat suitability for the species. Finding the species in diverse environments with different degrees of anthropogenic disturbance, seems to indicate a high tolerance of the Spectral Bat to habitat transformation. Additional information about diet and prey consumption, breeding patterns and home range in Colombia is non-existent; in

the same way, it was not possible to recover many field notes and data about the collection events.

Some recent records confirm the low detectability and local rarity of the Spectral Bat. The new record for the Department of Antioquia confirms the presence of the species that has not been registered since 1959 for the Urabá subregion (Cuartas-Calle and Muñoz-Arango 2003). Similarly, records after 35 years have been reported for the Department of Meta (Esquivel and Rodríguez-Bolaños 2018), despite several sampling efforts in both departments.

Forest cover is the most important factor behind *V. spectrum*'s distribution, and the response curves for this variable support this view – as has been suggested in other countries (Solari 2018). However, extremely high levels of forest cover reduced suitability, perhaps indicating a possible preference of the Spectral Bat for mosaic habitats. Precipitation in the driest month (Bio 14) was also very important for the species, with the response curves indicating higher levels of suitability for areas with high precipitation. These results suggest a potential vulnerability of *V. spectrum* to climate change effects in areas where temperature increases or precipitation decreases.

Although the ENM models produced high TSS and AUC scores, the ensemble maps should not be considered infallible. Factors such as human-wildlife conflict, competing species, dispersal limitations or stochastic processes can render climatically suitable areas unviable for *V. spectrum*. ENM methods can also be affected by unknown prevalence (the proportion of suitable sites occupied by the species), which can lead to misleading results (Guillera-Arroita et al. 2015). Our spatial rarefaction of the presence data should help to reduce the issue of sampling bias; however, the issue should not be considered completely resolved. Whereas they should not be considered infallible (especially for the thresholded map), they could nonetheless prove useful for planning future research and conservation actions.

Reviewed specimens show similar morphology and morphometrics, indicating little variability among the Colombian populations. The differences observed in the ear length and mean value of the forearm could be explained by the way the collectors historically took this measurement in the former and, in the latter, with clinal variation also observed in other bat species (Kelly et al. 2018). Specimens also showed variation in external characteristics such as fur coloration, ranging from grayish to reddish brown as have been previously recorded (Navarro and Wilson 1982). We are not able to define whether the differences between Colombian populations and northeast South America are associated with cryptic diversity within *V. spectrum*. However, further evidence and broader data analyses of the ear and forearm lengths should be explored to evaluate whether the differences are associated with clinal variation.

Conservation

The Spectral Bat is listed as Near Threatened by IUCN (Solari 2018), Vulnerable in Bolivia and Ecuador (Aguirre et al. 2009; Burneo et al. 2015) and Least Concern in Brazil (Instituto Chico Mendes de Conservação da Biodiversidade 2018). In Co-

lombia, the species is not included in any conservation plan, or a framework or protection policy. It is not included in the Red Book of Threatened Species (Rodríguez-Mahecha et al. 2006) or in the Threatened Fauna List of the Colombian government (Ministerio de Medio Ambiente y Desarrollo Sostenible 2017). Lack of information about natural history may be one of the main reasons why it is difficult to assess its conservation status. Likewise, the effectiveness of Protected Areas for the conservation of this species is not well known. Only three records (among 37) have been reported in these areas and our analyses show that only 13.06% of its suitable habitat area in Colombia is protected.

The key localities with capacity to contribute to the long-term survival of this species are mostly outside the boundaries of Protected Areas. In particular, we highlight the lack of PAs in the Andean region, because it is the region with the largest area of distribution in Colombia and an area quite threatened by the increasing human land use and habitat transformation. Protected areas are considered a central axis of national and international conservation strategies, becoming a fundamental tool to ensure the conservation of species and their ecosystems (Balmford et al. 2005). However, this study suggests that PAs are not providing efficient repositories for the species target conservation. This result is intended to help decision makers by identifying priority areas in which conservation efforts should focus.

Future studies should consider contributing to the knowledge of the natural history of this rare species. Widely unknown aspects such as habitat use and preference, population density, occupancy area and response to climate change should be a priority. The conservation of the Spectral Bat will depend on actions dedicated to the preservation and recovery of its habitat, to the formulation of Protected Areas and the development of environmental education activities. Likewise, the species should be included in plans of public or private areas where their presence has been recorded, as well as the protection of its identified shelters.

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Appendix 1

Natural History Museums examined. Reviewed personally* and online collections.**

Colección de Mamíferos del Instituto Alexander von Humboldt (IAvH), Villa de Leyva*
Colección de Mamíferos de la Universidad de Nariño (PSO-CZ), Pasto*
Colección Mastozoológica del Chocó (CMCH), Quibdó**
Colección de Mastozoología Universidad del Quindío (CMUQ), Armenia**
Colección Teriológica de la Universidad de Antioquia (CTUA), Medellín*
Colección Mastozoológica Universidad Industrial de Santander (UIS-MHN), Bucaramanga**
Colección Zoológica Universidad de Córdoba (CZUC), Montería*
Colección Zoológica Universidad del Tolima (CZUT), Ibagué*
Instituto de Ciencias Naturales (ICN), Universidad Nacional de Colombia, Bogotá*
Museo de Historia Natural Universidad Distrital Francisco José de Caldas (MUD), Bogotá*
Museo Javeriano de Historia Natural "Lorenzo Uribe, S.J." (MPUJ), Bogotá*
Museo de La Salle (MLS), Bogotá*
Museo de Historia Natural Universidad de Los Andes (Andes-M), Bogotá*
Museo de Historia Natural Universidad de Caldas (MHN-UCa), Manizales*
Museo de Historia Natural Universidad del Cauca (MHNUC), Popayán*
Universidad del Valle-Vertebrados Mamíferos (UV), Cali**.